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EEG frequency-tagging demonstrates increased left hemispheric involvement and crossmodal plasticity for face processing in congenitally deaf signers

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ABSTRACT

In humans, face-processing relies on a network of brain regions predominantly in the right occipito-temporal cortex. We tested congenitally deaf (CD) signers and matched hearing controls (HC) to investigate the experience dependence of the cortical organization of face processing. Specifically, we used EEG frequency-tagging to evaluate: (1) Face-Object Categorization, (2) Emotional Facial-Expression Discrimination and (3) Individual Face Discrimination. The EEG was recorded to visual stimuli presented at a rate of 6 Hz, with oddball stimuli at a rate of 1.2 Hz. In all three experiments and in both groups, significant face discriminative responses were found. Face-Object categorization was associated to a relative increased involvement of the left hemisphere in CD individuals compared to HC individuals. A similar trend was observed for Emotional Facial-Expression discrimination but not for Individual Face Discrimination. Source reconstruction suggested a greater activation of the auditory cortices in the CD group for Individual Face Discrimination. These findings suggest that the experience dependence of the relative contribution of the two hemispheres as well as crossmodal plasticity vary with different aspects of face processing.

1. Introduction

Face processing belongs to the most studied human brain functions, most likely due to the fact that faces play a unique role in social interactions (Calder et al., 2011). Faces convey crucial information about, e.g., the identity, sex, age, and emotional state of a person. The processing of faces recruits a network of brain regions which responds more strongly to faces than to other visual stimulus categories, mainly in the ventral occipito-temporal cortex (VOTC) and posterior superior temporal sulcus (pSTS) (Haxby et al., 2000; Duchaine and Yovel, 2015; Grill-Spector et al., 2017). Newborns display a bias for visual stimuli that encompass general statistical properties present in faces (e.g., "top-heavy patterns", Macchi Cassia et al. 2004; Simion et al., 2008). The face processing system specializes over an extended developmental period to the faces most often encountered (Macchi Cassia et al. 2009; Anzures et al., 2013).

An unsolved question is the extent to which different functions of the face processing system are shaped by experience. Here we investigated three sub-functions of face processing, in congenitally deaf individuals who all had learned a sign language as first language. Faces are of particular relevance to this population since on the one hand, facial cues are of special importance in sign languages and for lip reading, and on the other hand, deaf individuals miss vocal information to assess the emotional tone or identity of other people.

Following auditory deprivation, neural circuits which are associated with the deprived sensory system (i.e., the auditory cortex) as well as neural circuits, which represent the intact sensory input (e.g., the visual cortex) have been found to reorganize (Bavelier and Neville, 2002; Merabet and Pascual-Leone, 2010; Pavani and Röder, 2012; Heimler et al., 2014). These phenomena are called crossmodal and intramodal plasticity, respectively. Both crossmodal and intramodal plasticity have been linked to enhanced visual abilities in deaf individu-

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als (Bavelier et al., 2000; Bavelier et al., 2006; Lomber et al., 2010; Hauthal et al., 2013).

Studies on face processing in congenitally deaf signers have revealed both crossmodal and intramodal plasticity (McCullough et al., 2005; Stropahl et al., 2015; Benetti et al., 2017). A recent functional magnetic resonance (fMRI) study in congenitally deaf signers by Benetti et al. (2017) has investigated brain regions of the right superior temporal sulcus (STS), which have been suggested to comprise neural systems for voice processing (temporal voice area, TVA) in hearing individuals (Belin et al., 2000; Belin and Zatorre, 2003). Results revealed that the response of this area to faces was enhanced in deaf individuals as compared to both hearing signers and hearing non-signers. The authors interpreted their results in favour of the view that crossmodal plasticity follows the functional specialization of neural systems (Lomber et al., 2010): brain regions supporting person processing in one modality support person processing based on the remaining intact sensory modalities, if the typical modality input is missing. Moreover, the results of this study indicated that such crossmodal response could not be explained by the use of a sign language. McCullough et al. (2005) observed a change in the typical lateralization of ventral visual areas (specifically the fusiform gyrus) following congenital deafness: while emotional facial expressions elicited a bilateral activation of the fusiform gyrus (FG) in hearing controls, the activation was left lateralized in congenitally deaf signers (McCullough et al., 2005). This result suggests intramodal in addition to crossmodal changes of face processing in deaf individuals. Crucially, hearing native signers did not show a similar change in lateralization, suggesting that sign language experience alone was not responsible for these cortical changes (Emmorey and McCullough, 2009). In sum, these studies provide evidence that the human face processing system depends on early experience (Bettger et al., 1997; McCullough et al., 2005; Weisberg et al., 2012; Letourneau and Mitchell, 2013; Benetti et al., 2017). In concordance with a change in the lateralization of neural systems related to face processing, behavioural studies have shown a reduced left visual field (LVF) bias in early deaf individuals when judging emotional facial expressions of the gender of faces (Letourneau and Mitchell, 2013; Dole et al., 2017). By contrast, the typical LVF bias was observed in deaf signers for face identity judgments (Letourneau and Mitchell, 2013) suggesting that changes in laterality are task dependant.

However, which face processing functions are experience-dependent and whether different functions encounter distinct neural adaptations is yet unknown. To address these questions, the same subjects must be tested for different face processing functions. This approach was implemented in the present study by employing Fast Periodic Visual Stimulation (FPVS) and recording triggered changes in the electroencephalography (EEG) in a group of congenitally deaf signers and a group of hearing controls. The two groups were compared in three functions of face processing: (1) the ability to discriminate faces from non-face objects, i.e. Face-Object Categorization, (2) the ability to discriminate changes in facial expression i.e. Emotional Facial Expression Discrimination, and (3) the ability to individuate face identities, i.e. Individual Face Discrimination. We used FPVS-EEG since visual stimuli presented at periodic rates typically elicit high signal-to-noise ratio (SNR) responses over the human scalp which can be objectively quantified in the frequency-domain (see Norcia et al., 2015; Rossion et al., 2020 for reviews). In recent years, this approach has been successfully used to provide sensitive and objective measures of face processing in typically developed individuals (Rossion et al., 2020 for a recent review). This technique allowed us here to measure rapidly and objectively robust discriminative responses within the same participants and within the same experimental session. We exploited this powerful technique to investigate the combined impact of a congenital auditory deprivation and the use of a sign language since birth on different face processing functions.

All experiments implemented in the present study were previously validated in hearing individuals (Liu-Shuang et al., 2014; Rossion et al., 2015; Dzhelyova et al., 2017). Pictures were presented at a fixed rate of 6 Hz (six images/s) with a target stimulus being presented every five stimuli (i.e. 6/5 = 1.2 Hz). The target was defined as a face among other objects in experiment 1; a face with an emotional expression among neutral faces in experiment 2 and the image of a face having a different identity among images of faces having the same identity in experiment 3. In experiment 2 and experiment 3, images were selected from the same dataset, but stimulus categories were orthogonally organised: while in the Emotional Facial Expression Discrimination experiment the identity of the faces was randomized across facial expressions, in the Individual Face Discrimination experiment emotional facial expressions were randomized across face identities. Therefore, by using the same set of stimuli, we were able to directly compare neural correlates of emotion vs. identity processing between congenitally deaf signers and hearing adults. For each of the three experiments, neural responses at the target frequency (1.2) Hz and its harmonics were extracted from the EEG frequency-domain representation. The overall discriminative response was compared between the two groups. Based on previous findings (McCullough et al., 2005; Letourneau and Mitchell, 2013), we predicted a relatively stronger involvement of the left hemisphere for face categorization and for aspects of face processing related to sign language (the processing of facial expressions) but not to identity. Crossmodal plasticity, that is, a stronger activation of the auditory cortex in response to face stimuli, was assessed with distributed sources modelling. We hypothesized that congenitally deaf signers would activate the auditory cortex more than controls during face processing (Benetti et al., 2017; Stropahl et al., 2015).

2. Methods

2.1. Participants

Twelve congenitally deaf adults (from now on referred to as “CD”, eight men, mean age = 25.15 years, SD = 4.02, range: 21–33 years; all of them completed secondary schools) participated in the present study. All CD participants were right-handed and had a profound bilateral hereditary deafness with a hearing loss greater than 100 dB in the better ear since birth. All participants had learned a sign language as first language. Ten deaf participants had acquired German Sign Language (*Deutsche Gebärdensprache*, DGS; Kubus et al., 2015) as their first language while the two remaining participants had learned Turkish or Russian Sign Language as their first language. These two participants had acquired DGS as a second sign language and used DGS as their main language. DGS proficiency was assessed with the German Sign Language Repetition Task (DGS-SRT; see Supplementary Material) by two deaf experts who were native signers. According to the DGS-SRT evaluation, all deaf participants owned native-like DGS competence. All CD participants were recruited from the North German region, had normal or corrected-to-normal vision, and none of them reported a history of a neurological disorder.

A control group of twelve hearing non-signers (from now on referred as “HC”, eight men, mean age = 25.36 years, SD = 3.54, range: 20–32 years) matching the CD individuals in age, gender and handedness, was recruited from the local community of the city of Hamburg, Germany. All hearing participants had normal or corrected-to-normal vision and reported that they had never suffered from any neurological disorder.

The study was approved by the ethical committee of the German Society of Psychology and was conducted in accordance with the seventh revision of the Declaration of Helsinki. Prior to testing, all participants received instructions about the experimental procedure (for the CD individuals, the explanation was provided in written from and in a DGS video) and gave their written informed consent.

2.2. Experimental design and setup

The study consisted of three previously validated EEG experiments: (1) Face-Object Categorization (FO; from Rossion et al., 2015),

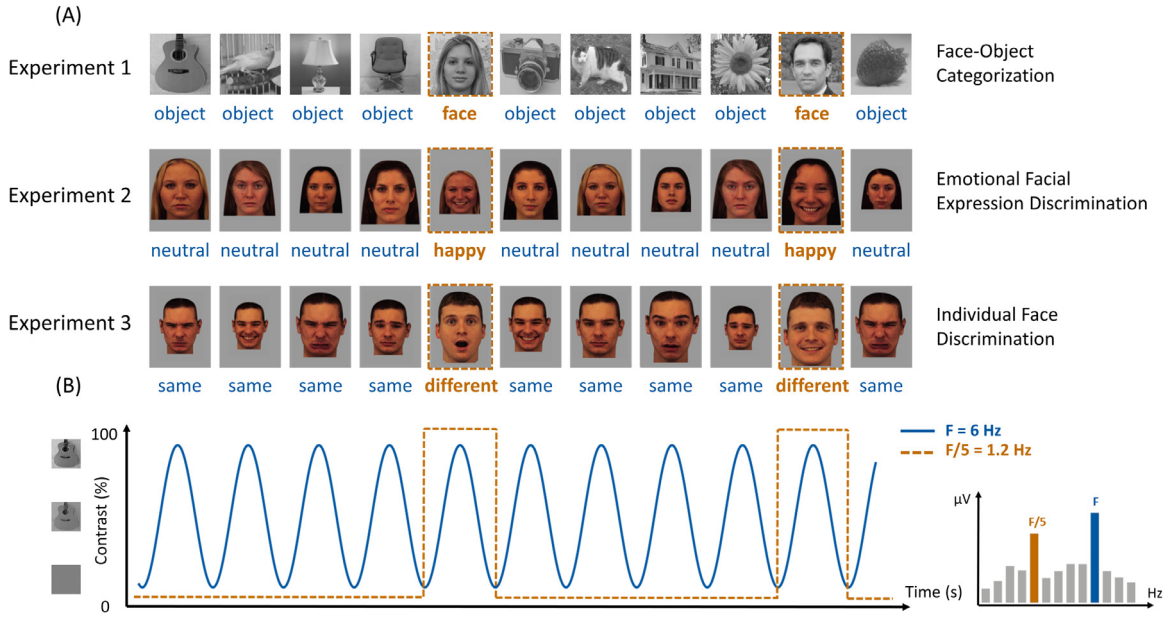

Fig. 1. Schematic illustration of the experimental paradigms (for details see Liu-Shuang et al., 2014; Rossion et al., 2015; Dzhelyova et al., 2017). (A) All three experiments shared a similar design. Stimuli were presented at a base frequency of 6 Hz (solid blue line in B). Key stimuli appeared periodically every fifth image, that is, at a rate of 1.2 Hz (dashed orange line in B). *Experiment 1: Face-Object Categorization (FO).* Stimuli included grey-coloured images of non-face objects from ten different categories and images of faces. The stimulus appearing every 5 stimuli was always a face. *Experiment 2: Emotional Facial Expression Discrimination (EM).* Neutrally expressive faces of different identities were presented at the base frequency, whereas expressive faces with another emotion (disgust, fear or happiness) appeared at the oddball frequency (identity was changing for each image). *Experiment 3: Individual Face Discrimination (ID).* Stimuli included Face images of different identities with neutral or expressive emotions (fear, disgust, happiness). At the base frequency, different expressions of the same face-identity were presented, while at the oddball frequency, a novel identity was used (emotional facial expression was changing for each image). In all three experiments, participants continuously monitored a colour-change of a small cross located at the centre of the visual stimuli to which they had to respond with the button-press. (B) An illustration of the sinusoidal contrast modulation used for stimuli presentation and the periodic response (that is, a periodic EEG response to a fast periodic visual stimulation, appearing at the same frequency as the stimulation); the response at the base frequency is indicated with the blue colour, whereas the oddball response is indicated with the orange colour. Note: responses at the corresponding harmonics are not shown on the figure.

(2) Emotional Facial Expression Discrimination (EM; from Dzhelyova et al., 2017) and (3) Individual Face Discrimination (ID; from Liu-Shuang et al., 2014; as extensively reviewed in Rossion et al., 2020).

Each participant performed all three experiments during one session, in a dimly lit room in the Biological Psychology and Neuropsychology lab of the University of Hamburg. The order of the experiments was the same for every participant: FO, ID and EM. However, we report methods and results of each experiment with the following order FO, EM, ID as it better represents the hierarchy within the face processing system. The stimuli were delivered on a Dell computer monitor with 1680 × 1050 resolution and a refresh rate of 60 Hz, by adopting a sinusoidal contrast modulation (0–100%) at 6 Hz using the Sinstim Toolbox created in Matlab 2009 (MathWorks Inc., Natick, MA). Thus, each stimulation cycle lasted 167 ms. The full luminance value of each pixel of an image was reached around 83 ms after the onset of a stimulus, that is, at half cycle.

During EEG recording, participants were comfortably sitting at 80 cm viewing distance from the computer screen. Prior to testing, participants were instructed to adopt a relaxed sitting position, to refrain from moving and to continuously fixate on a small black cross (16 pixels resolution, 5 mm in size, 0.35° of visual angle) shown at the centre of the flickering stimuli (the fixating cross was located between the eyes of the faces). Participants were asked to detect infrequent changes (from black to red) of the fixation cross and to press the space-bar of a keyboard (placed in front of them) with the index finger of the right hand whenever the fixation cross changed its colour. Participants were instructed to perform this colour detection task without ignoring the stream of images in the background. Colour changes occurred 10 times per stimulation sequence at random times. Response times (RT) and accuracy (percentage correct) to colour changes were recorded. During the EEG session, a webcam continuously monitored participants to guarantee continuous communication between them and the experimenter. Participants were invited to take regular breaks every 10–15 min and to shortly rest after each sequence (see *Procedure*). When a participant was ready for the next sequence, he/she made a sign towards the camera upon which the experimenter started the next sequence. The sequence order was randomized for each participant. The total testing time, including three experiments with EEG application/removal, breaks, took about 3 h.

Face-Object Categorization (experiment 1)

2.3. Stimuli

Fifty-one photographic images of faces and 254 photographic images of various objects (animals, plants, houses, and human-made objects) were used as stimuli (see Experiment 1 in Fig. 1). All images were in greyscale, equalized in luminance and contrast, 200 × 200 pixels in size (for the details on the stimuli data-set, see (Rossion et al., 2015). The stimuli were shown on the screen within an area of 7.3 × 7.3 cm at the resolution of 259 × 259 pixels, resulting in a 5.22° of visual angle (VA) when viewed at a distance of 80 cm. The faces were unknown to the participants and they had not seen any of the object pictures prior to the experiment.

2.4. Procedure

Stimulus presentation was controlled using Matlab 2009. Fast Periodic Visual Stimulation (FPVS, Rossion, 2014b) was applied, with sinusoidal contrast modulation at the base frequency of 6 Hz. A face image appeared after four images of other objects, that is, at a frequency of

1.2 Hz. To compose a sequence, the stimulus selection for both stimulus categories was random. Frequencies of interest included the base frequency (6 Hz), the oddball frequency (1.2 Hz), and harmonics for the oddball frequency (e.g., 2.4 Hz, 3.6 Hz, etc.).

Stimulation sequences were shown to test the ability to discriminate between the face-stimuli and other objects from other categories. Since multiple object identities were used, categorization required generalizing across multiple face exemplars and objects. The amplitude of the EEG signal at the 1.2 Hz frequency and its harmonics was considered as an indicator of category discrimination and generalisation (Rossion et al., 2018).

Each sequence was repeated twice for each participant. Each sequence lasted for 64 s, including 60 s of stimulation, 2 s of fading-in and 2 s of fading-out, at the beginning and at the end of stimulation. Only these 60 s of "pure" stimulation were further analysed. Each sequence start was preceded by the appearance of a small black fixation cross against the grey blank background for 2–5 s (randomly jittered in length), in order to setup and maintain the participants' eye-fixation.

Emotional Facial Expression Discrimination (across identities; experiment 2)

The stimuli used in experiment 2 and experiment 3 were selected from the same stimulus set. For Emotional Facial Expressions Discrimination, neutrally expressive faces were presented at the base frequency, while a face expressing disgust, fear or happiness was shown at the oddball frequency (see Experiment 2 in Fig. 1). For both the base and the oddball frequency the identity of the face was randomized; gender was kept constant.

2.5. Stimuli

Due to time constraints, we limited the investigation to the discrimination of three emotional facial expressions (namely, fear, disgust and happiness) with respect to a neutral facial expression. Fourteen full coloured front face pictures from the Karolinska Directed Emotional Faces dataset were selected (Lundqvist et al., 1998) comprising 7 males and 7 female identities with 4 facial expressions: 3 emotional expressions corresponding to fear, disgust, and happiness plus 1 neutral. Therefore, 56 stimuli were used in total. Participants were unfamiliar with the pictures prior to testing. Each face picture had an equalized mean pixel luminance during stimulation. The original background was replaced with a grey colour.

2.6. Procedure

The base frequency was generated by presenting images randomly selected from 7 different identities (either from the male or female pool) with a neutral emotional facial expression. Every fifth stimulus (oddball), a face with one of three emotional expressions was shown (while the identity of the face was random). Within a stimulation sequence, the same emotional facial expression was used as oddball images (that is either disgust, fear, or happiness). To avoid low-level repetition effects, the size of the pictures was randomly varied between 90% and 110% at every stimulation cycle (Dzhelyova and Rossion, 2014a, Dzhelyova and Rossion, 2014b).

The number of sequences was 6: 3 oddball emotional expressions (disgusted, fearful, and happiness) and 2 experimental conditions (upright and inverted). Each sequence was repeated 4 times (2 sequences of male identities and 2 of female identities), resulting in a total of 24 randomised sequences. The inverted condition was used as a control. Stimulus selection for both stimulus categories was random. All images were 300 × 450 pixels in size. The stimuli were shown on the screen within an area of 8.5 × 12.7 cm, resulting in 6° of visual angle (VA) when viewed at a distance of 80 cm. Each sequence lasted 54 s, including 50 s of stimulation, 2 s of gradual fading-in at the beginning and 2 s of gradual fading-out at the end of stimulation. Only 50 s of stimulation were included in the data analysis. The remaining procedure was as for experiment 1. Without counting breaks, the duration of the experiment lasted for about 21 min (24 sequences × 54 s).

Individual Face Discrimination experiment

2.7. Stimuli

For Individual Face Discrimination (experiment 3), at the base frequency different expressions of the same identity were presented, whereas at the oddball frequency, a novel identity was used. The stimuli were extracted by the same set of stimuli which was used in experiment 2. To maximize the generalizability of the identity discrimination across the largest possible sets of different images, we used all emotional facial expressions which were available in the set of stimuli: 7 males and 7 female identities, each with 7 facial expressions (fear, angry, disgust, happiness, neutral, sad, and surprised). Thus, in total 98 pictures were employed. Participants were unfamiliar with the pictures prior to testing. Images were presented with the same size as in experiment 2, all other parameters were as in experiments 1 and 2.

2.8. Procedure

Two conditions were implemented (upright and inverted) with four repetitions per condition (2 sequences with male identities and 2 sequences with female identities), resulting in a total of 8 randomised sequences. The base frequency was generated by presenting images randomly selected among 7 different facial expressions of the same identity; every fifth face, another identity (oddball frequency; 6 Hz/5 = 1.2 Hz) was shown. At the start of each sequence, the base identity was randomly selected from four possible identities. The face identities presented at the oddball frequency were randomly selected from the remaining pool (i.e., from 42 pictures: 6 different identities with 7 different emotional expressions each).

To avoid low-level repetition effects, the size of the pictures was randomly varied between 90% and 110% at every stimulation cycle (Dzhelyova and Rossion, 2014a, Dzhelyova and Rossion, 2014b). To further isolate face individuation responses that cannot be accounted merely by physical differences between images, we used an inverted face presentation as a control condition, in which the same face stimuli were used albeit upside-down (note: Fig. 1 shows only upright condition of experiment 3).

Each sequence lasted 54 s, including 50 s of stimulation, 2 s of gradual fading-in at the beginning and 2 s of gradual fading-out at the end of stimulation. Only the 50 s of stimulation were included to further data analysis. The remaining procedure was as described for Experiment 1 and 2. Without counting breaks, the duration of the experiment lasted for about 7.2 min (8 sequences × 54 s).

2.9. EEG acquisition

The EEG was recorded with 74 Ag/AgCl passive electrodes (Easycap) referenced to the right earlobe and acquired using the BrainVision software (Brain Products, GmbH). The sampling rate was 500 Hz (hardware bandpass filter with a passband of 0.032–200 Hz). Electrode positions included standard international 10–20 system locations and additional intermediate positions (see supplementary Fig. S1).

2.10. Data analysis in the frequency-domain

The analysis in the frequency domain was performed in Letswave 6 (Matlab-based toolbox; http://www.nocions.org/letswave). The same pre-processing procedures (tuned for the Fast Periodic Visual Stimulation) were applied to the datasets of all three experiments, according to most recent studies with such paradigms (e.g., Yan et al., 2019; Retter et al., 2020; see also the review of Rossion et al., 2020). First, a Butterworth bandpass filter was applied to the EEG data (fourth-order, 0.1–120 Hz cut-off), which was down-sampled from 500 to 250 Hz, and

segmented from −2 s to 66 s in order to include 2 s of recording before the first stimulus onset and 2 s after the end of each sequence. For each participant, recording sequences of each experiment were concatenated (separately for each experiment). Biological artefacts related to eye-movements and eye blinks were removed by applying an independent component analysis on the extended Infomax (Bell and Sejnowski, 1995; Jung et al., 2000a, 2000b). Components were extracted and then inspected for their spectral properties, scalp distribution, and distribution across sequences. ICA components indicating one of the artefacts listed above were removed. Noisy channels were replaced by interpolating 3 neighbouring channels (Experiment 1 (FO): 3 channels in total across 2 CD participants and 8 channels in total across 6 HC participants; Experiment 2 (EM): 13 channels in total across 9 CD participants and 9 channels in total across 6 HC participants; Experiment 3 (ID): 7 channels in total across 5 CD participants and 4 channels in total across 4 HC participants). All channels were finally re-referenced to a common average reference. At the single participant level, each epoch was further segmented to an integer number of 1.2 Hz cycles, starting at the onset of the sequence and lasting 60 s (corresponding to 72 cycles, 15,000 time points in total, in FO experiment) or 50 s (corresponding to 60 cycles, 12,500 time points in total, in EM and ID experiments). This procedure was applied to avoid spectral leakage to neighbouring frequencies. The number of bins for a frequency of interest was computed through a Matlab custom made script *integercycle*, multiplying the value of the sampling rate by the length of the segment. To increase SNR, epochs corresponding to stimulation sequences of the same condition were averaged in the time domain, separately for each participant. Fast Fourier Transform (FFT) was applied to each of the averaged segments, converting the EEG data to the frequency domain. The FFT transformation yielded a spectrum ranging from 0 to 250 Hz with a spectral resolution (i.e. frequency bins) of 1/60 s, i.e. 0.017 Hz for FO experiment and 1/50 s, i.e. 0.02 Hz for the EM and the ID experiments.

To quantify the responses of interest, we first identified in each experiment whether there was a significant response at the frequency of interest (e.g. 1.2 Hz) and its harmonics. To this aim, we computed the FFT grand averaged data across participants, conditions, and groups, separately for each experiment. The amplitude of the FFT data was further averaged across all electrodes. The amplitude value at the fundamental frequencies of interest (1.2 Hz or 6 Hz) and their harmonics (2.4 Hz, 3.6 Hz, etc.; 12 Hz, etc.) was compared to the distribution calculated on the amplitude of the FFT grand averaged data measured at 20 surrounding bins (of each frequency of interest). We excluded the 2 bins (one on the left and one on the right side) immediately adjacent to the frequency of interest, to exclude potential amplitude leakage across adjacent bins (Dzhelyova and Rossion 2014a, Dzhelyova and Rossion, 2014b; Retter and Rossion 2016). Z-values were then computed separately for each frequency of interest, against the surrounding noise (note that, in both groups and across all experiments and conditions, the distributions of the amplitudes of surrounding bins were normally distributed). Z-values were calculated as follows: the amplitude at the frequency of interest (e.g. 1.2 Hz) MINUS the average of surrounding bins / standard deviation of surrounding bins. This procedure measures the deviation of the amplitude of the frequency of interest with respect to the mean of the surrounding bins, expressed in terms of standard deviations from this mean. Frequency bins with a z-value larger than 1.64 (corresponding to a one-tailed p-value of $p < 0.05$) were considered as deviating significantly from noise. A one-tailed liberal statistical threshold was used at this stage to select the highest number of harmonics to obtain an accurate quantification of the signal, with a one-tailed testing due to the directionality of the hypothesis (i.e., signal > noise level; see Rossion et al., 2020; see also Supplementary Material for a data analysis performed using a more stringent Z-value of 3.29, corresponding to a two-tailed p-value of $p < 0.001$ with similar results). Once significant responses at the frequencies of interest (e.g. 1.2 Hz, 2.4 Hz, and so on) were identified, we returned to the raw single subject data and computed baseline-correction for each participant and condition. Only for frequencies which differed from surrounding noise (in the FFT grand averaged data across participants, conditions and groups) the baseline correction was computed at the single participant level as follows: from the frequency of interest the averaged amplitude of 20 surrounding frequency bins (10 from each side) was subtracted (we did not consider immediately adjacent bins, which might contain power in the frequency of interest due to a spectral leakage, and the local maximum and minimum amplitude bins as in (Dzhelyova and Rossion 2014a, Dzhelyova and Rossion, 2014b; Retter and Rossion 2016). Moreover, for visualization purposes, the SNR was calculated for each participant and condition as follows: the amplitude at the frequency of interest was divided by the average amplitude of 20 surrounding bins (we did not consider the same bins which were excluded in the baseline-correction procedure, see above). This procedure was implemented to correct for the overall noise level and to better visualise the data (Dzhelyova et al., 2017).

For each frequency of interest, we then identified the set of consecutively significant baseline-corrected harmonics in the FFT grand averaged data across participants, conditions, and groups. Harmonics of the 1.2 Hz oddball frequency, which corresponded to the base frequency or its harmonics, the 5th (6 Hz), 10th (12 Hz), and 15th (18 Hz) were not considered, because the responses to stimuli presented at both base and oddball frequencies are confounded at these frequencies. These significant harmonics were then combined into a summed oddball response at the single participant level. Once the summed oddball response was averaged for each participant, it was used as a dependent measure for further statistical analyses (see Dzhelyova et al., 2017). In the FO experiment (experiment 1), 14 consecutive harmonics (i.e. 1.2 Hz to 20.4 Hz; see Supplementary Material) were significant. In the EM experiment (experiment 2) 18 consecutive harmonics (i.e. 1.2 Hz to 26.4 Hz; see Supplementary Material) were significant. The summed oddball response across emotional facial-expressions was calculated by averaging the summed oddball response calculated at the level of single Emotional Facial-Expressions in each group. Finally, for in the ID experiment, the significant summed oddball response was composed by the average first 6 harmonics (i.e. 1.2 to 8.4 Hz; see Supplementary Material; see also Rossion et al., 2020). Finally, we computed grand averages of both baseline-corrected and SNR data across participants for each group and condition.

The main aim of the frequency domain analyses was to perform between group comparisons of the summed oddball responses. The analysis focused on the average of the response across posterior electrodes in the left and right hemisphere, which for both groups comprised the highest baseline-corrected amplitudes in each experiment (see Supplementary Fig. S1). Data inspection revealed a strong consistency between the scalp topographies measured in the present sample of HC individuals and previous studies using the same paradigms (e.g. Liu-Shuang et al., 2014; Rossion et al., 2015; Dzhelyova et al., 2017). Electrode selection included four pairs (P7-P8, PO7-PO8, P9-P10, PO9-PO10) covering the posterior lateral portions of left and right hemispheres. At the single participant level, data were averaged across selected electrodes separately for each hemisphere. The resulting amplitude values were used for statistical comparisons. For each of the three experiments, we separately ran a mixed-design analyses of variance (ANOVAs; IBM SPSS Statistics V21.0.0) with group (CD, HC) as between-participant factor and the following within participant factors: For FO experiment: Hemisphere (left, right); for EM experiment: Condition (upright, inverted), Hemisphere (left, right); for ID experiment: Condition (upright, inverted), Hemisphere (left, right).

For the FO experiment, the analyses at posterior electrodes aimed at specifically testing for the two-way Hemisphere*Group interaction effect (Condition as a factor was not present in this experiment) and, we limited the analysis to this pre-specified effect (as opposed to investigating all main effects and interactions as it is done in exploratory analyses; see Cramer et al., 2016). For EM and ID experiments, at posterior electrodes we aimed at testing for the two-way Hemisphere*Group and,

for the three-way Hemisphere*Condition*Group interaction effects, and the analyses were limited only to these pre-specified effects (see Cramer et al., 2016). *P*-values were corrected for multiple comparisons across selected F tests (i.e. interactions listed above) using the false discovery rate (FDR; Benjamini et al., 2001). Moreover, for each participant, a laterality index (LI) was calculated separately for each experiment as follows: Laterality Index=(L-R)/(|L|+|R|). Negative and positive values indicate a greater involvement of the right and of the left hemisphere, respectively (see e.g., Seghier et al., 2008). At the single participant level, L and R represent the EEG responses measured over each hemisphere averaged across the selected posterior electrodes. For both EM and ID experiments the LI was assessed only for the upright face conditions. At the group level, LI greater than a threshold of |0.2| indicated that there is at least a 50% higher activity in one hemisphere than in the other hemisphere. This threshold has been previously suggested as indicating hemispheric dominance (see Seghier et al., 2008).

Prior to performing the analysis in the source space we assessed at the scalp level potential crossmodal activations in the CD group by analysing the responses measured at the vertex cluster comprising the midline electrodes FCz, Cz and CPz (that is, electrodes typically measuring the maximal responses from the auditory cortex; see Supplementary Figure 1). The same statistical models were run as for the posterior electrodes albeit without the factor Hemisphere. The two-way ANOVAs which were run for vertex responses in the experiments EM and ID aimed at exclusively testing for a possible Condition*Group interaction (see Cramer et al., 2016). In the result section we reported only these pre-specified effects. For Post hoc analyses conducted to further analyse significant pre-specified interactions we used planned pairwise comparisons (Bonferroni corrected). Since the analysis at the vertex was exploratory before employing source modelling, we did not apply a correction for running two-mixed-design ANOVAs within the same experiment.

As control analyses, for each of the three experiments we ran ANOVAs using as dependent measure the response measured at the base frequency (6 Hz and its harmonics, 12 Hz and 18 Hz). This analysis focused on the same electrodes used for the summed oddball response.

2.11. Data analysis in the time-domain

The time-domain analysis was conducted with two main aims: (a) to visualize the time-course of the EEG response in all three experiments; (b) to perform an analysis in the source space (source modelling). The latter was not performed in the EM experiment as different emotional expressions are known to elicit different scalp topographies (Dzhelyova et al., 2017; Leleu et al., 2018) and source modelling of each emotional facial expression was beyond the scope of the present study.

The time-domain analysis was performed by implementing the pipeline used by Stropahl et al. (2015), Stropahl et al. (2018). Raw EEG data were pre-processed with EEGLAB 13.6.5 b (Delorme and Makeig, 2004). First, a low pass filter (windowed sinc FIR filter, cut-off frequency 40 Hz, filter order 500) as well as a high pass filter (windowed sinc FIR filter, cut-off frequency 1 Hz, filter order 100; (Widmann et al., 2015) were applied. Data were resampled to 250 Hz. In order to remove non-stereotypical artefacts (such as sudden increases of muscle activity) from the data, continuous datasets were segmented into consecutive epochs with a length of 1 s. Segments displaying a joint probability of activity (Delorme et al., 2007) larger than three standard deviations (SD) were removed before performing the ICA. To remove typical artefacts such as eye movements and eye blinks, an independent component analysis based on the extended Infomax (Bell and Sejnowski, 1995; Jung et al., 2000a, 2000b) was performed. In order to reduce computational time, the number of decomposed components was reduced from 74 to 50. The ICA weights were then associated to the raw EEG (continuous and unfiltered data). ICA components representing artefacts were identified with the semi-automatic algorithm CORRMAP (Viola et al., 2009). Following artefact-related component removal the data were segmented accordingly to stimulus presentation. Consecutive epochs with a length of 0.7 s (−0.2 to 0.5 s) were generated. Epochs were time-locked to the 0% contrast time-point in the sinusoidal contrast modulation. In the ID experiment, epochs were calculated for the presentation of all face stimuli, but only for the upright condition. In order to match the SNR-level between the brain responses to different stimulus categories, in the FO experiment, only object images presented immediately before face stimuli were selected. Analogous to the FO experiment, only the face stimuli having the same identity, presented immediately before the face having a new identity were considered. Epochs having a joint probability of activity greater than four standard deviations (Stropahl et al., 2018) were automatically rejected (mean epochs removed per condition and group were: FO: CD = 9.2%, SD=3.3; HC=8.1%, SD=2.1; ID: CD = 8.9%, SD=1.5; HC=8.6%, SD=1.8). Finally, the data were baseline corrected using the −100 to 0 ms pre-stimulus period, and digitally filtered (low-pass filter with a 40-Hz upper cut-off, order 100).

To visualize the time-course of the EEG signals, consecutive epochs with a length of 5.6 s (0 to 5.6 s) were extracted from the data after artefact-related component removal. The first 15 cycles of stimulation from the start of each sequence (3 times AAAAB sequences) were discarded from analyses, to only include EEG signal in which the periodic response had already been built. Each 5.6 s segment included 6 repetitions of the AAAAB sequence. At the individual subject level, epochs were averaged and low-pass filtered at 20 Hz (note that for both groups all significant harmonics occurred below 20 Hz). The data extraction was carried at the individual level separately for each experiment and condition. Data were then averaged at the group level for visualization (see Supplementary Figs. 3–5). EEG segments revealed a highly structured non-linear response in the time domain.

2.12. Source reconstruction

Source estimation was performed using Brainstorm software (Tadel et al., 2011), which is based on a distributed dipoles model fitting approach. Sources were extracted by applying a dynamic statistical parametric mapping (dSPM; Dale et al., 2000), which has been shown to provide a better localization of deep sources than standard minimum norm procedures (Lin et al., 2006). The dSPM adopts minimum-norm inverse maps to estimate the locations of scalp electrical activities. Before source estimation, the EEG data were re-referenced to the common average reference (Michel et al., 2004). Moreover, the activity was normalized by an estimate at the individual level of the noise standard deviation at each electrode location (Hansen et al., 2010). To this end, for each participant and location, noise covariance matrices and individual noise standard deviations were calculated using single trials baseline intervals data (−100 to 0 ms). The boundary element method (BEM) provided in OpenMEEG was adopted as a head model (default parameters in Brainstorm were selected). The BEM provides anatomical information by three realistic layers (Gramfort et al., 2010; Stenroos et al., 2014). Source estimation was performed by selecting the option of constrained dipole orientations (Tadel et al., 2011). Single-trial data were averaged for each individual, then the estimate of active sources was calculated at the individual level.

Based on the existing literature (Finney et al., 2001; Sandmann et al., 2012; Cardin et al., 2013; Bottari et al., 2014; Stropahl et al., 2015) an Auditory region of interest (ROI) was defined a priori in each hemisphere before any statistical comparison was run (see Supplementary Figure S2). Estimated activations of this ROI were used to compare congenitally deaf individuals (CD) and hearing controls (HC). The ROIs were defined by using the Destrieux-atlas (Destrieux et al., 2010; Tadel et al., 2011), as implemented in FreeSurfer (http://ftp.nmr.mgh.harvard.edu/fswiki/CorticalParcellation), which is available in Brainstorm and adopts an automatic parcellation performed by a surface-based alignment of the cortical folding (Destrieux et al., 2010). The Auditory ROI was defined by combining three areas to include Brodmann areas 41 and 42 (Destrieux: G_temp_sup-G_T_transv,

S_temporal_transverse and G_temp_sup-Plan_tempo). The so defined Auditory ROI has repeatedly shown crossmodal activations in deaf individuals (Finney et al., 2003; Sandmann et al., 2012; Cardin et al., 2013; Bottari et al., 2014; Stropahl et al., 2015).

First, source estimates in the Auditory ROIs were analysed for the FO and the ID experiments within each group. For the FO experiment we compared, separately for each hemisphere, the source estimates in response to faces and to objects within the 200–300 ms time-window (see supplementary Fig. 6) and, for the ID experiment the source estimates in response to the different and the same face identities within the 300–400 ms time-window (see supplementary Fig. 7). Two-sided *t*-tests for dependent samples were performed at each time-point within these preselected time windows. False discovery rate (FDR; Genovese et al., 2002) was used to correct for multiple comparisons. FDR bound (q-value) was set at 0.05 (Genovese et al., 2002). Note that, in the FO experiment, the latency of the source peak in response to faces was consistent with the original ERP result found in the study by Rossion et al. (2015) at posterior scalp location (i.e. 220 ms).

Second, source estimates of the evoked response to faces in the FO experiment and in response to different face identities in the ID experiment were compared between groups in the auditory ROIs. A specific hypothesis was tested in both FO and ID experiments. Based on previous evidence, we hypothesized that the CD group would show greater activations of the auditory cortex as compared to the HC group (Bottari et al., 2014; Stropahl et al., 2015; Benetti et al., 2017). To test this hypothesis, direct comparisons were performed between source activations measured in the Auditory ROIs, separately for each hemisphere. Local maxima (i.e., the absolute peak magnitude of source activations measured in Auditory ROIs) of the responses to faces (FO experiment) and different face identities (ID experiment) occurred for both groups, within the significant within-group effects (faces vs. objects: see supplementary Fig. 6; same vs. different face identities: see Supplementary Fig. 7). Thus, local maxima for faces and different face identities were used as landmarks for the between group comparisons. One-sided *t*-tests for independent samples were performed at each time-point within 50 ms time windows which comprised for each experiment the local maxima of both groups. For the FO experiment, the 50 ms time-window was between 210 and 260 ms and for the ID experiment between 340 and 390 ms. False discovery rate (FDR; Genovese et al., 2002) was used to correct for multiple comparisons. FDR bound (q-value) was set at 0.05 (Genovese et al., 2002). For all analyses, tests with *p*-values smaller than the FDR corrected *p*-values were considered as significant.

2.13. Behavioural data

For each participant and experiment, we calculated the mean accuracy (percentage of correct responses) and the mean RT for the detection of the colour change of the fixation cross. As control analyses, two separate ANOVAs (IBM SPSS Statistics V21.0.0) were run using as dependent measures of accuracy and RT for each experiment (FO, EM, ID). For both EM and ID experiments, the ANOVAs included Condition (upright and inverted) as within-participants factors and Group (CD and HC) as between-participants factor.

3. Results

3.1. Experiment 1 (Face-Object categorization, FO)

3.1.1. Behavioural results

Two separate one way ANOVAs with Group (CD and HC) as between-participants factor revealed that CD and HC groups did not differ in the mean accuracy or in mean detection times (mean accuracy: all *p*-values > 0.1; CD group = 97.9%, SD = 0.03%; HC group = 99.6%, SD = 0.01%; mean RTs: all *p*-values > 0.3; CD = 416 ms, SD = 59 ms; HC = 396 ms, SD = 45 ms).

3.1.2. Face-selective response

As expected, based on previous studies, the face-selective response appeared predominantly in the right hemisphere in HC (mean amplitudes: left hemisphere = 3.1 μV; SE = 0.42; right hemisphere = 3.6 μV; SE = 0.44). In contrast, the face-selective response was more pronounced in the left hemisphere in the CD group (left hemisphere = 3.5 μV, SE = 0.55; right hemisphere = 2.9 μV, SE = 0.28; see Fig. 2). This observation was confirmed by an ANOVA with Hemisphere (left and right) as within-participants factors and Group (CD and HC) as between-participants factor, showing a significant interaction between the two factors ($F(1,22) = 4.4$, $p < 0.05$, $\eta_p^2 = 0.17$). Despite the significant interaction, post-hoc pairwise comparisons did not reveal a greater response in the left hemisphere for the CD group than in the HC group, and no greater response in the right hemisphere for the HC group compared to the CD group (all *p* values > 0.1, corrected). Moreover, post-hoc pairwise comparisons did not reveal a greater response in the left hemisphere vs. the right hemisphere for the CD group, nor a greater response in the right hemisphere as compared to the left hemisphere for the HC group (all *p* values > 0.1, corrected; LI was below the |0.2| threshold for both the CD and the HC group). No between group differences emerged at the vertex (see methods section; all p-values > 0.8).

3.2. Experiment 2 (Emotional facial expressions discrimination, EM)

3.2.1. Behavioural results

The ANOVAs with Condition (upright and inverted) as a within-participants factor and Group (CD, HC) as between-participants factor did not reveal an effect of Group, neither for accuracy (all *p*-values > 0.08; CD = 96.2%, SD = 6.3%; HC = 97.8%, SD = 2.9%;) nor for mean detection times (all *p*-values > 0.1; mean RT: CD = 431 ms, SD = 60 ms; HC = 419 ms, SD = 46 ms).

3.2.2. Response to facial expression change

In HC, the facial expression response appeared as bilateral over posterior electrodes (left hemisphere = 0.8 μV, SE = 0.24; right hemisphere = 0.8 μV, SE = 0.13), whereas it appeared as being predominantly involving the left hemisphere in the CD group (left hemisphere = 1.1 μV, SE = 0.18; right hemisphere = 0.8 μV, SE = 0.05; see Fig. 3). The mixed-design ANOVA with Condition (upright and inverted) and Hemisphere (left and right) as within-participants factors, and Group (CD and HC) did not reveal significant effects for Hemisphere and Group interaction or the Hemisphere, Condition and Group interaction (all p values > 0.1; see Fig. 3). However, planned pairwise comparisons revealed that the HC group had a bilateral response for both upright and inverted conditions (left vs. right hemisphere comparison for upright: $F(1,22) = 0.14$, $p > 0.7$, $\eta_p^2 = 0.01$, corrected; inverted: $F(1,22) = 0.56$, $p > 0.4$, $\eta_p^2 = 0.02$, corrected) while a tendency toward a stronger involvement of the left hemisphere was found in the CD group selectively for the upright conditions (left vs. right hemisphere comparison for upright: $F(1,22) = 3.5$, $p = 0.07$, $\eta_p^2 = 0.14$, corrected; inverted: $F(1,22) = 0.11$, $p > 0.7$, $\eta_p^2 = 0.01$, corrected; see Fig. 3C; LI was below the |0.2| threshold for both CD and HC groups). Finally, no significant interaction between the factors Condition and Group emerged at the vertex (all p-values > 0.7).

3.3. Experiment 3 (Individual face discrimination, ID)

3.3.1. Behavioural results

A mixed-design ANOVA with Condition (Upright and Inverted) as within-participants factor and Group (CD, and HC) as between-participants factor did not indicate any significant main effect or interactions involving the factor Group for accuracy or RT measures (mean accuracy: all *p*-values > 0.08; CD = 97.3%, SD = 4.1%; HC = 96.4%, SD = 3.8%; mean RT: all *p*-values > 0.2; CD = 437 ms, SD = 51 ms; HC = 426 ms, SD = 53 ms).

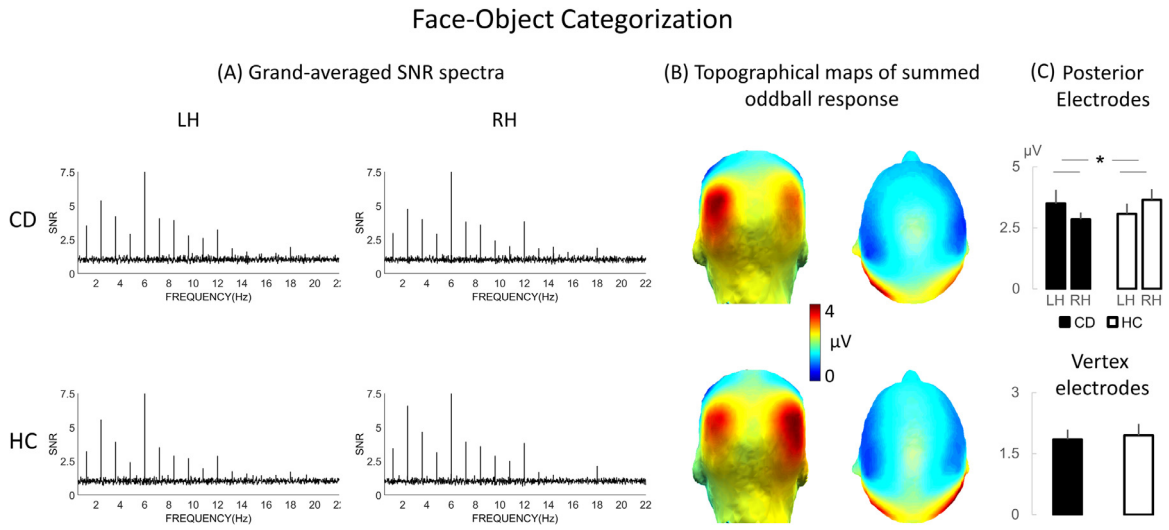

Fig. 2. Experiment 1 (Face-Object Categorization): CD, congenitally deaf group; HC, hearing control group. (A) Grand-averaged SNR spectra across posterior electrodes in the left and in the right hemisphere. (B) Topographical maps (from back and top views) of the grand-averaged summed oddball response (baseline-subtracted amplitudes). (C) Upper panel: the bar plot shows the response measured at left and right hemispheres at the posterior electrodes for the summed oddball response to face stimuli for both groups. Bottom panel: the bar plot displays the response measured in each group at the vertex. Error bars represent standard errors of the mean. The statistically significant interaction is marked with "*" ($p < 0.05$).

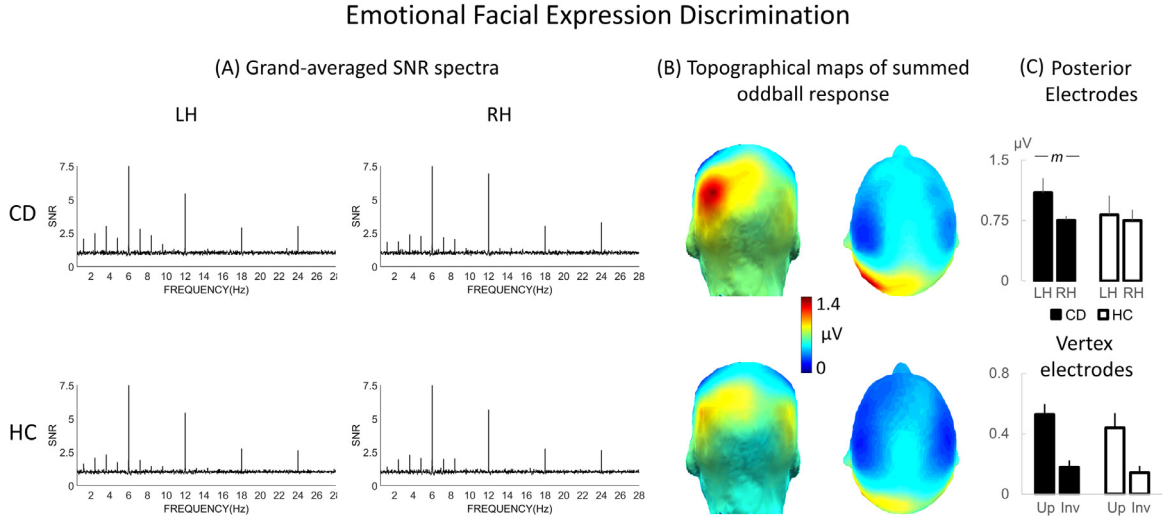

Fig. 3. Experiment 2 (Emotional Facial Expression Discrimination): response to changes across facial expressions (from neutral to either fear, happiness, or disgust). CD, congenitally deaf group; HC, hearing control group. (A) Grand-averaged SNR spectra averaged across emotional facial-expressions (disgust, fear, and happiness), in the upright condition for across posterior electrodes in the left and in the right hemisphere. (B) Topographical maps (from back and top views) of the grand-averaged summed oddball response (baseline-subtracted amplitudes), averaged across emotional facial-expressions, in the Upright condition for both groups. (C) Upper panel: The bar plot shows the response measured across posterior electrodes in the left and right hemispheres of the grand-averaged summed oddball response mean amplitudes, averaged across emotional facial-expressions, in the Upright condition for the two groups. Bottom panel: displays the grand-averaged summed oddball response mean amplitudes measured at the vertex for each Group as a function of Condition (Upright and Inverted). Error bars represent standard errors of the mean. The tendency towards a significant post-hoc comparison is marked with "*m*".

3.3.2. Identity discrimination response

The scalp topographies indicated a slight increase in amplitude over the right compared to the left hemisphere for HC (left hemisphere = 0.87 μV, SE = 0.20; right hemisphere = 1.04 μV, SE = 0.16) this was also found in the CD group (left hemisphere = 1.07 μV, SE = 0.13; right hemisphere = 1.13 μV, SE = 0.11; see Fig. 4). The mixed ANOVA with Condition (upright and inverted), Hemisphere (left and right) as within-participants factors, and Group (CD and HC) as between-participants factor did not reveal significant pre-selected interactions involving the factors Hemisphere and Group (all $p > 0.4$; see Fig. 4). Planned pairwise comparisons revealed that for both the HC group (HC left vs. right hemisphere, upright: $F(1,22) = 1.4$, $p > 0.2$, $\eta_p^2 = 0.06$, corrected; inverted: $F(1,22) = 3.9$, $p > 0.05$, $\eta_p^2 = 0.15$; corrected) and the CD group (CD left vs. right hemisphere, upright: $F(1,22) = 0.2$, $p > 0.6$, $\eta_p^2 = 0.01$, corrected, inverted: $F(1,22) = 2.2$, $p > 0.1$, $\eta_p^2 = 0.09$, corrected) the response in the left and right hemispheres did not differ (see Fig. 4C upper panel; LI was below the |0.2| threshold for both CD and HC groups). However, a significant interaction between the factors Condition and Group emerged at the vertex ($F(1,22) = 4.7$, $p < 0.05$, $\eta_p^2 = 0.17$). Post-hoc pairwise comparisons showed that both groups had a greater response for the upright as compared to inverted Condition (p values < 0.001, corrected). Moreover, post-hoc pairwise comparisons did not reveal a between group effect for either the Upright or for the Inverted Condition (all p values > 0.1, corrected). Thus, the CD group

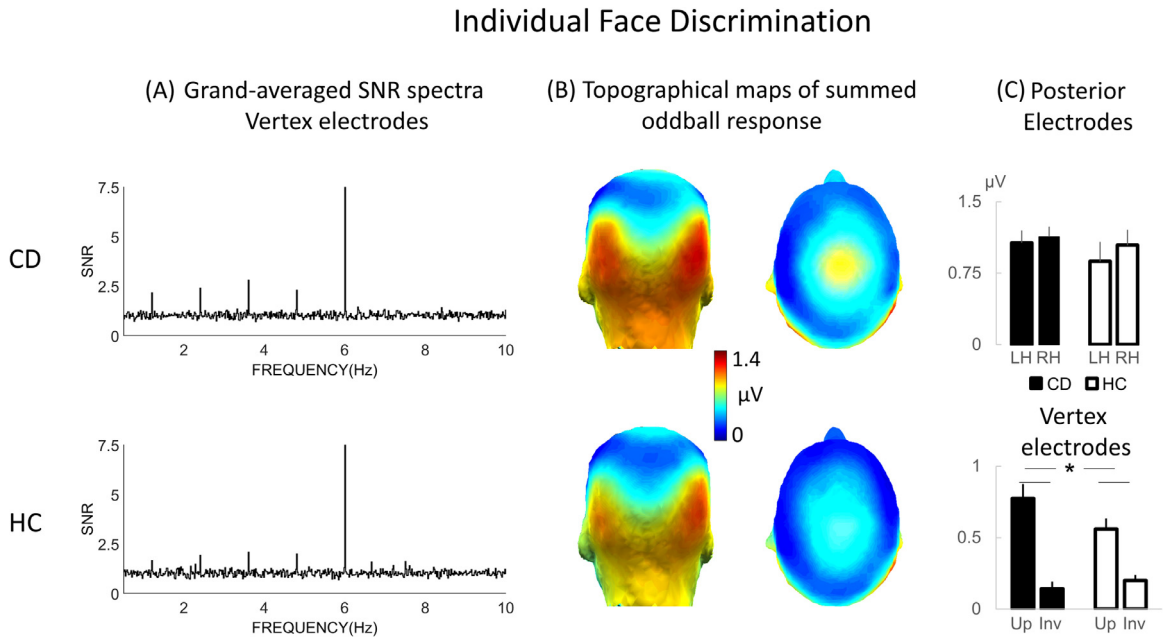

Fig. 4. Experiment 3 (Individual Face Discrimination): response to face identity change. (A) Grand-averaged SNR spectra for the central electrode FCz in the upright condition. (B) Topographical maps (from back and top views) of the grand-averaged data show the summed oddball response (baseline-subtracted amplitudes) to a face identity change, in the Upright condition. (C) The bar plot shows the grand-averaged summed oddball response associated to face identity change, (upper panel) at posterior electrodes for left and right hemispheres (in the Upright condition), and (Bottom panel) at the central cluster of electrodes for Upright and Inverted conditions in congenitally deaf (CD) and hearing (HC) participants. Error bars represent standard errors of the mean. Statistically significant interaction involving the Group factor is marked with "*" ($p < 0.05$).

displayed a greater difference between the response to the upright and the inverted conditions (CD: mean upright minus inverted = 0.61 μV, SE = 0.09) compared to the HC group (HC: upright minus inverted: mean = 0.35 μV, SE = 0.08; see Fig. 4C lower panel).

3.3.3. Base frequency

As complementary analyses, a series of ANOVAs with Hemisphere (left and right) and, if appropriate, Condition (Upright and Inverted, for the EM and the ID experiment) as within-participant factors and Group (CD and HC) as between-participant factor were run for each experiment for the responses measured at the base frequency. No significant interactions involving the factor group emerged (all *p*-values > 0.2). The same analyses performed at the vertex found no significant difference between group (all p-values > 0.3).

3.3.4. Source estimates for FO and ID experiments at auditory ROIs

For each experiment, direct between group comparisons were performed with running t-tests between source activations measured in the Auditory ROI of each hemisphere (significant effects were FDR corrected). Comparisons were performed within a 50 ms time-window comprising local maxima of both groups (time windows: FO: 210–260 ms; ID: 310–360 ms; see Method section; for within group comparisons see Supplementary Material). Source estimates of the two groups were compared for the response to faces in the FO experiment and for the response to different face identities in the ID experiment. The analyses aimed at assessing whether a greater response at the pre-defined Auditory ROIs was found in the CD group as compared to the HC group.

3.3.5. Experiment 1 (Face-Object categorization, FO)

No significant differences emerged for the between group comparison performed on the sources estimated in the Auditory ROIs (see Fig. 5).

Experiment 3 (Individual Face Discrimination, ID)

The between-group comparison of the estimated source activity in the Auditory ROIs revealed that congenitally deaf individuals displayed a greater activation to different face identities as compared to hearing

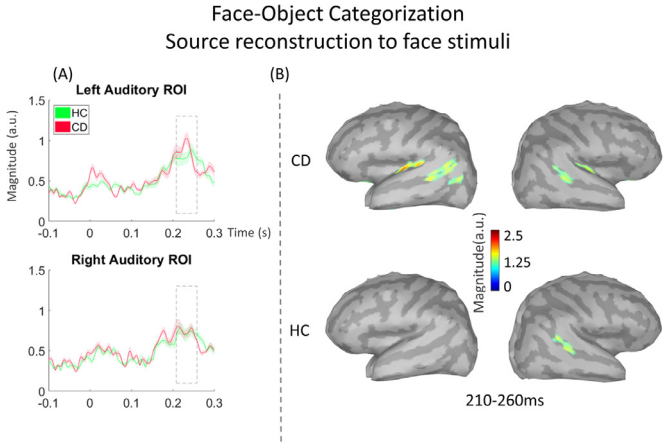

Fig. 5. Source analysis performed in the time domain for the Face-Object Categorization experiment. Activity is shown in response to face stimuli. (A) From top to bottom: the time course of the activity measured for each group at left and right Auditory ROIs. Grey dashed boxes represent the time-window of interest (210–260 ms). (B) Source activities averaged within the 210–260 ms time window for CD group (top) and HC group (bottom). Source activities are represented as absolute values and in arbitrary units based on the normalization within the dSPM algorithm. The colour bar indicates the magnitude of activation. No between-group differences emerged.

controls in the right hemisphere (time points with $p < 0.05$, FDR corrected are highlighted in grey in Fig. 6A).

3.4. Discussion

The present study investigated the experience dependence of the development of three aspects of face processing: (i) Face-Object Categorization (faces vs. objects of different categories; experiment 1), (ii)

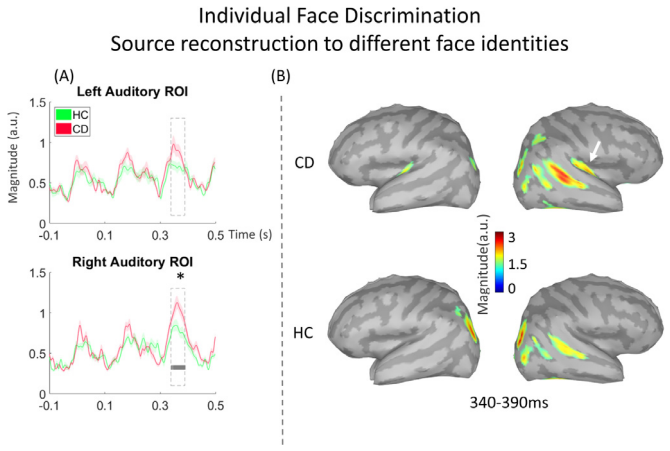

Fig. 6. Source analysis performed in the time domain for the Individual Face Discrimination experiment. Activity is shown in response to the change of face identity. (A) From top to bottom: the time course of the activity measured for each group at left and right Auditory ROIs. Grey dashed boxes represent the time-window of interest (340–390 ms). (B) Source activities averaged within the 50 ms time-window (340–390 ms) for the CD group (top) and the HC group (bottom). The grey box highlights the duration of significant group differences (FDR corrected). The CD group revealed a greater response to changes of face identity in the right Auditory ROI compared to the HC group. Source activities are represented as absolute values and as arbitrary units based on the normalization within the dSPM algorithm. The colour bar indicates the magnitude of activation. Statistically significant effects are marked with "*" ($p < 0.05$, corrected).

Emotional Facial Expression Discrimination (emotional faces vs. neutral faces; experiment 2), and (iii) Individual Face Discrimination (different vs. same face identities; experiment 3). To this end, we recorded the EEG in three experiments involving fast periodic visual stimulation (FPVS; Rossion, 2014b; Rossion et al., 2015) in a group of congenitally deaf signers (CD) and a group of matched hearing controls (HC).

There is evidence that face processing has distinct neural correlates in deaf signers compared to hearing controls (McCullough et al., 2005; Benetti et al., 2017). However, a systematic assessment of the neural correlates of different aspects of face processing in the same individuals has been lacking. Here, for each experiment, we compared the neural response of the two groups at posterior lateral electrode locations, which have been demonstrated to best capture the responses associated to face categorization, emotional facial expression and identity discrimination (see Liu-Shuang et al., 2014; Rossion, 2014b; Rossion et al., 2015; Dzhelyova et al., 2017). This approach allowed us to investigate the functional organization of different aspects of face processing within the same subjects. Face categorization elicited a relatively stronger involvement of the left hemisphere in the CD group than the HC group. The same trend was observed for the EM experiment but not for the ID experiment.

Changes in the relative hemispheric involvement of neural systems such as for motion processing (Bavelier et al., 2001; Bosworth and Dobkins, 2002; Brozinsky and Bavelier, 2004), visual spatial attention (Neville and Lawson, 1987a) and language processing (Neville and Bavelier, 1998) have previously been observed in congenitally deaf signers. For instance, in a visual spatial attention task, a left hemispheric dominance was found in deaf individuals (Neville and Lawson, 1987b), which was only partially related to the usage of a sign language - hearing native signers displayed the typical right hemispheric dominance (Neville and Lawson, 1987a, 1987c). In contrast, changes in visual field dominance for motion processing have been found in both deaf and hearing signers, but not in hearing non-signers, suggesting a crucial role of sign languages for the development of the neural representations of visual motion (Bosworth and Dobkins, 2002). Furthermore, in an fMRI study, deaf signers did not display the typical hemispheric dominance of left-hemisphere language regions (e.g., inferior frontal gyrus, posterior superior temporal gyrus) during a reading task, but a rather bilateral response in the middle temporal and temporo-parietal cortices (Neville et al., 1998). However, more recent studies have suggested that language proficiency might explain some of these results: deaf individuals who were highly proficient users of both a sign language and a written language have displayed a typical left hemispheric dominance for reading (MacSweeney et al., 2002; Skotara et al., 2012; Hänel-Faulhaber et al. 2014).

Changes in the responses measured in the two hemispheres for face processing have been previously observed in congenitally deaf native signers (McCullough et al., 2005; Weisberg et al., 2012). In an fMRI study, Weisberg et al. (2012) showed a reduced selectivity to faces relative to houses in deaf signers as compared to hearing non-signers in the right fusiform gyrus, whereas the two groups had a similar response in the left fusiform gyrus. However, Benetti et al. (2017) did not report lateralization differences between early deaf individuals and hearing control for face categorization (faces vs. houses). These inconsistent results might be accounted for the different deaf individuals who took part in these experiments. While in the first study (Weisberg et al., 2012) congenitally deaf individuals were native users of a sign language, in the study of Benetti et al. (2017) deaf participants had acquired a sign language at different years of age. Our sample resembled the deaf participants of Weisberg et al. (2012), and so did the observed shift towards a greater involvement of the left hemisphere for face categorization. These results might indicate that a combination of native acquisition of a sign language and congenital deafness results in a change of the representation of face categorization.

In the fMRI study of McCullough et al. (2005) brain activation in response to emotional and linguistic facial expressions was assessed in deaf native signers and hearing non-signers. The authors found that in deaf signers, both tasks elicited a left-lateralized fusiform gyrus activation, whereas hearing non-signers displayed a bilateral activation. The authors speculated that this change in functional lateralization might be due to the crucial role of facial movements in expressive sign language (McCullough et al., 2005). However, the finding that hearing native signers did not show a similarly alternated lateralization later questioned this interpretation (Emmorey and McCullough, 2009). The results of both the FO and EM experiments from the present study support an increased involvement of the left hemisphere for face processing in congenitally deaf native signers. Given that we did not test a group of hearing individuals who started acquiring a sign language from birth, we are not able to disentangle the effects of deafness and of early sign language acquisition on the neural representation of face processing. Future research including hearing native signers should address the specific impact of the analyses of linguistic facial expressions occurring in sign languages on the neural representation of face processing. Moreover, because we analysed neural responses at predefined scalp locations, we might have missed additional group differences, such as enhanced amygdala responses which have been previously observed (Weisberg et al., 2012).

Studies on the role of literacy in shaping the functional organization of the brain have provided evidence that learning to read has an impact on the neural organization of other parts of the visual system than only those typically associated with reading (Dehaene et al., 2015). Specifically, while the right hemispheric lateralization for face categorization emerges in infancy well before reading acquisition (de Heering and Rossion, 2015), competition with the processing of written text when children start to read seems to further contribute to the right hemisphere specialization for face processing (Dehaene et al., 2010). The neural competition hypothesis was supported by the observation that in children, high reading proficiency was accompanied by a stronger right lateralization of face categorization (Dundas et al., 2015; Lochy et al., 2019). A recent EEG study tested deaf individuals and hearing controls, who were matched in their reading abilities

(Emmorey et al., 2017). Interestingly, higher reading skills were associated with a stronger left hemispheric activity in hearing individuals but with a stronger right hemispheric activity in deaf individuals. The authors interpreted these findings as supporting the phonological mapping hypothesis, which proposes that left hemispheric processing of word-form predominantly emerges to link orthography and phonology, that is visual word form areas (VWFA) and auditory language regions (McCandliss and Noble, 2003). In sum, these results might suggest that the lack of speech input changes the cerebral organization with regard to reading and in turn alters the lateralization of the face processing system in congenitally deaf individuals. However, not all results have been in consistence with this view. No differences in the VWFA activation have been found in response to written text in congenitally deaf signers and hearing controls, suggesting that in deaf individuals the neural correlates of reading are not necessarily altered (Waters et al., 2007; Emmorey et al., 2013; Wang et al., 2015). Moreover, it is noteworthy that the hemispheric specialization for face categorization does not follow a linear development (Lochy et al., 2019). From being right lateralized in newborns (de Heering and Rossion 2015), it seems to encounter a bilateral phase in 5-year old children (Lochy et al., 2019; but see Cantlon et al., 2011) before resulting in the adult-like right hemispheric dominance. The associated developmental trajectory as well as the impact of literacy need yet to be further investigated in deaf individuals.

The Individual Face Discrimination experiment revealed other group differences between the CD and the HC group than the Face Object categorization and Emotional Facial Expression Discrimination experiments. No differences were found between groups in the hemispheric responses. A previous behavioural study (Letourneau and Mitchell, 2013) showed a left visual field (LVF) bias for both an emotional facial-expressions judgement and a face identity classification task in hearing individuals. By contrast, deaf signers showed an RVF bias for the judgments of emotional facial-expressions, but the typical LVF bias for face Identity judgments. The present study possibly provides the neural correlates for these behavioural group differences. The lack of group differences in the lateralization for face identity processing of the present study suggests either less experience dependence or no dependence on auditory input or speech. Facial cues play a dominant role in person recognition (Sheehan and Nachman, 2014). In fact, not all patients with lesions in the right ventral cortex have additional difficulties recognizing others from their voices (Gainotti and Marra, 2011); some patients with prosopagnosia have been found to even outperform healthy controls in voice recognition tasks (Hoover et al., 2010).

However, Individual Face Discrimination selectively yielded responses compatible with crossmodal plasticity in the right auditory cortex of CD individuals. This result is in accordance with findings of right auditory cortex activation in deaf individuals in response to visual stimuli (Finney et al., 2001; Sandmann et al., 2012). Furthermore, it is in line with the results of a recent fMRI adaptation study, in which a group of early deaf individuals showed a higher selectivity for face individuation in the right temporal voice area (TVA; Belin and Zatorre, 2003) compared to hearing controls (Benetti et al., 2017). However, in the present study the Auditory ROI was defined by combining three areas to include Brodmann areas 41 and 42 (Finney et al., 2003; Sandmann et al., 2012; Cardin et al., 2013; Bottari et al., 2014; Stropahl et al., 2015), which are located less laterally and ventrally with respect to the right temporal voice area (TVA). Finally, it is noteworthy that the time-course of source estimates of the present study depends on the paradigm used, which comprised (i) periodic stimulations and (ii) periodic contrast changes (rather than abrupt onsets). Thus, the time-course of source estimates cannot be directly compared to other studies with different stimulation methods (see Rossion et al., 2015 for a discussion on this aspect).

In sum, our results suggest that different aspects of the neural systems associated with face processing show specific experience dependent functional organizations - they adapt partially in different ways to altered experience. These adaptations comprise intramodal plasticity (changes in the hemispheric involvement of the visual cortex) or crossmodal plasticity (stronger activation of what is typically auditory cortex).

Declaration of Competing Interest

The authors declare no competing financial interests.

CRediT authorship contribution statement

Davide Bottari: Conceptualization, Data curation, Formal analysis, Writing - original draft, Writing - review & editing. **Evgenia Bednaya:** Formal analysis, Writing - original draft, Writing - review & editing. **Giulia Dormal:** Conceptualization, Methodology, Funding acquisition, Formal analysis, Writing - review & editing. **Agnes Villwock:** Writing - review & editing. **Milena Dzhelyova:** Writing - review & editing. **Konstantin Grin:** Writing - review & editing. **Pietro Pietrini:** Writing - review & editing. **Emiliano Ricciardi:** Writing - review & editing. **Bruno Rossion:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing. **Brigitte Röder:** Conceptualization, Funding acquisition, Writing - original draft, Writing - review & editing.

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The datasets and code used in the current study are available from the corresponding author on reasonable request.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2020.117315.

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